

# A comparison between affiliative and agonistic behaviours in wild and captive *Sapajus libidinosus* (Spix, 1823) (Mammalia, Primates, Cebidae)

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**Abstract.** Organisms modulate the expression of their behaviours through environmental contexts. Several studies have suggested that the frequencies of social behaviours may differ between captive and free-living primates. In the present study, we compared the social behaviours displayed by captive and free-living groups of the bearded capuchin monkey (*Sapajus libidinosus*), describing and analysing their social behaviours. We observed through focal animal sampling 59 animals distributed in 10 social groups, analysing 191:45 h of videos of their behaviours. Captivity reduced the frequency of agonistic, but not of affiliative behaviours. Furthermore, neither group size nor sex could explain the overall variability in affiliative behaviour. We conclude that captivity has indeed an important impact only on some aspects of social behaviour, namely, on agonistic behaviours.

**Keywords.** Capuchin monkeys; Free-living; Neotropical primates; Sociality.

## INTRODUCTION

Primate social groups are hierarchically structured, so that the behaviour displayed by each individual reflects its social position, and hence its role within the group (Carvalho, 2008). Given their dominance-based hierarchy, primate social groups are frequently dominated by few individuals with preferential access to resources (such as reproductive opportunities, access to food, protection from other individuals), and with greater chances of reproductive success (Fedigan, 1993; Jurmain & Nelson, 1994). Notwithstanding the social constraints derived from a hierarchical organisation, the variety of social interactions (agonistic, affiliative) and contexts (feeding, parental care, resting, mating) connected to social life provide opportunities for a broad variety of interactions among group members (Jolly, 1985; Casanova, 2006; Boyd & Silk, 2009).

In general, social relations in primates are established in two ways, through agonistic (conflicts and/or threats) and affiliative behaviour (Fragaszy *et al.*, 2004). Aggression and affiliation are evident features of life in most primate social groups

(Carpenter, 1942). Affiliative behaviours include positive associations, social proximity, social gathering, social play, reconciliations and sexual behaviours (Fragaszy *et al.*, 2004), while agonism refers to behaviours that range from threat and submission to attack and struggle (Huntingford & Chellappa, 2011).

Affiliative behaviours represent more than 80% of the time budget for social activities in primates (Sussman *et al.*, 2005). As such, affiliative behaviours play an important role in forming social alliances between individuals and are important for maintaining complex primate social systems, reducing competition within groups, increasing the likelihood of accessing resources, relieving social tensions after aggression (Mitani & Watts, 2010) and maintaining or improving social status within a group (Surbeck & Hohmann, 2011), eventually leading to reproductive gains (Pope, 2000; Surbeck & Hohmann, 2011).

In turn, agonistic behaviours are relatively rare in primates, composing usually less than 1% of the time budget for social activities (Sussman *et al.*, 2005). Aggressions are generally related to group hierarchy (Fragaszy *et al.*, 2004; Ferreira

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*et al.*, 2006), with dominant individuals frequently involved in these interactions, often as aggressors of subordinate individuals (Sapolsky, 2005). Agonism is fundamental for the formation and maintenance of groups (De Waal, 2005), and food competition is the main ecological factor for the increase of agonistic behaviours (Crook & Gartland, 1966; Eisenberg *et al.*, 1972; Dittus, 1977; Janson, 1988). Adaptively, the hierarchy would be a “regulator for a system of privileges, usually measured by observing agonistic acts between the dyads, in determining leadership, to resolve conflicts or even to avoid excessive aggression” (Jorge & Collaço, 2008).

On top of the hierarchical constraints on social behaviour, it has been suggested that relevant contextual factors, such as captivity versus free-living conditions, would modulate social interactions. For example, it has been shown that living in high densities (a condition usually associated to captivity) tends to increase the frequency and duration of affiliative and prosocial behaviours, a result associated with increased agonistic interactions, mainly between females (De Waal, 1989; Judge & De Waal, 1997). Subsequent studies found nevertheless that crowding (higher confinement) had no effect on aggression, and a marginal effect on affiliative behaviour (only male-female grooming increased) (Judge *et al.*, 2006). Captive males show high standards of tolerance, considering that they can live in captivity for years without a single physical agonistic event, a situation at odds with observations in natural settings; in addition, captive alpha males can maintain their status in the group for much longer than wild alpha males, a result interpreted as a consequence of reduced agonism and increased time devoted to play and grooming interactions, possibly as a consequence of the favourable captivity conditions on the quantity and distribution of food resources (Fragaszy *et al.*, 2004).

These putative social behaviour differences between wild and captive primates could be related to a variety of contextual factors. The documentation of social behaviours in primates appears mostly either in studies focussing on a group in captivity or, alternatively, in studies that focus on a free-living group. More rarely we find empirical studies focussing simultaneously on multiple groups (or populations, see for example Izar *et al.*, 2012). However, up to now we found no study aiming to test empirically the effect of captivity on primate social behaviour by measuring simultaneously distinct wild and distinct captive groups. While the comparison between results from (available studies focussing on) wild groups and results from (available studies focussing on) captive groups is certainly feasible, any conclusion regarding the effect of captivity on social behaviour spanning from such a systematic review of multiple studies should necessarily rely on the control of a variety of inter-studies differences (Hedges & Olkin, 2014). Some differences are difficult to handle, such as studies that use ethograms beyond comparison, while others are more amenable to statistic controls, such as studies that focus on distinct species (Adams & Collyer, 2018), or that use different ecological or behavioural sampling protocols. A simpler

solution, one that we follow here, is the direct and simultaneous measurement of behaviour in various social groups, under both wild and captive conditions. Directly comparing animal activity budgets across distinct environmental conditions may provide a reliable assessment on the context-specificity of primate behaviour (*i.e.*, behavioural repertoire breadth) and on the frequencies at which different behaviours are performed (Howell & Cheyne, 2019).

Here we compare the expression of social behaviours in captive and free-living groups of bearded capuchin monkeys, *Sapajus libidinosus* (Primates, Cebidae). They are considered the most intelligent Neotropical primates, showing behavioural traditions and tool use (Ottoni, 2009; Falótico & Ottoni, 2013; Falótico *et al.*, 2017; Visalberghi *et al.*, 2017; Falótico *et al.*, 2018). Bearded Capuchin monkeys (*S. libidinosus*), as well as other species of the genus, exhibit multimale/multifemale social organisation with a dominant male controlling food access while being responsible for group defence and mating (Fragaszy *et al.*, 2004; Izar *et al.*, 2012; Verderane *et al.*, 2013). In addition, capuchin monkeys organise themselves into matrilineal systems, with the possibility of fission-fusion in periods of food shortages (Izar *et al.*, 2012). They have a polygynous mating system in which the females even request copulation from dominant males, making facial expressions, specific vocalisations and postural displays (Di Bitetti & Janson, 2001; Visalberghi & Fragaszy, 2002; Carosi *et al.*, 2005; Falótico & Ottoni, 2013). As is common among primates, grooming is a frequent affiliative behaviour (Izar, 1994). The social structure is based on separate dominance hierarchies among males and females, and involves a series of affiliative, cooperative and agonistic behaviours (Tiddi *et al.*, 2012; Scarry, 2013). Their groups are behaviourally plastic in relation to the variety of environments they occupy (Ottoni & Mannu, 2001; Fragaszy *et al.*, 2004) and to their social structure (Izar & Ferreira, 2007).

In the present study, we tested for differences in affiliative and agonistic behaviours between captive and wild individuals. We also analysed whether group size and gender influence these putative differences between wild and captive animals. Following the rationale above, we hypothesised that captive animals should have a higher proportion of affiliative interactions, while wild animals should show a higher proportion of agonistic behaviours.

## MATERIAL AND METHODS

### Study sites

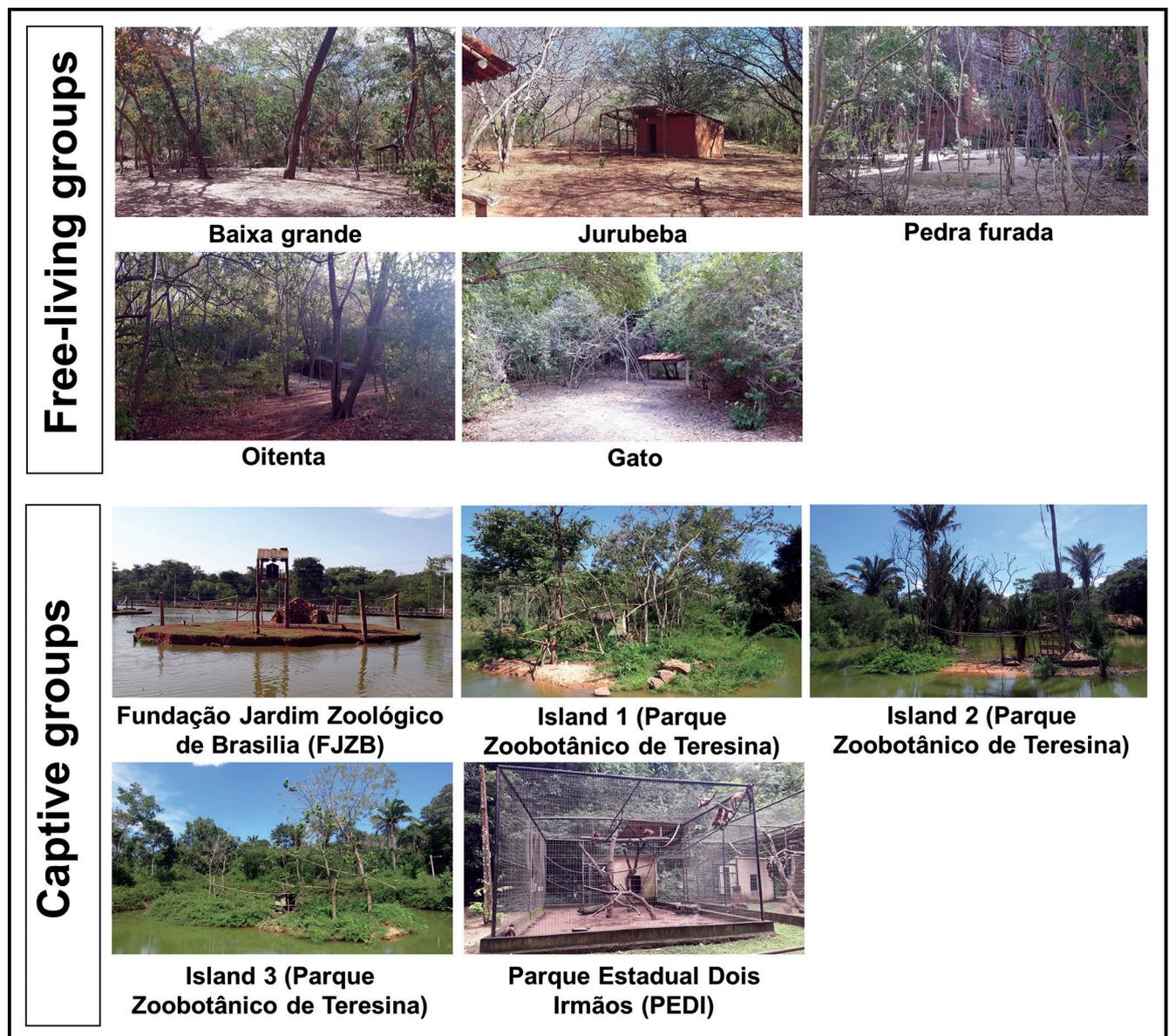
We compared *S. libidinosus* social behaviours under two main conditions: free-living and captivity. Five free-living groups were studied at Parque Nacional Serra da Capivara (Piauí State), three captive groups were studied at the Parque Zoobotânico de Teresina (Piauí State), one group in the Parque Estadual Dois Irmãos (Pernambuco State), and one group in the Fundação

Jardim Zoológico de Brasília (Distrito Federal). Given the timescale of the study, each group can be considered independent from the others, since there was no record of any type of contact between members of the different groups during the study.

The Parque Nacional Serra da Capivara is located in the municipality of São Raimundo Nonato, Piauí State, north-eastern Brazil (Appendix 1, Fig. 1). The park is a Brazilian integral protection area, with an area of 100,764.19 hectares. It is located in the south-east of Piauí within the Caatinga biome. The mean annual temperature is 28°C, with June presented coldest month, the mean temperature ranging 25°C-35°C. In the beginning of the rainy season, in October and November, the park presents warmest periods of the year, with a mean temperature varying from 31°C to 47°C. The mean annual precipitation is 689 mm ([https://www.wikiparques.org/wiki/Parque\\_Nacional\\_da\\_Serra\\_da\\_Capivara](https://www.wikiparques.org/wiki/Parque_Nacional_da_Serra_da_Capivara)). All

groups of monkeys, as well as other animals in the park, are provisioned with corn and bananas, three times a week, during the driest months of the year (June to October), using an artificial feeder made of concrete. Only the Pedra Furada group has contact with tourists. The other free-living groups only have contact with researchers.

The three groups of capuchin monkeys (Appendix 1, Fig. 1) living in the Parque Zoobotânico de Teresina (PZT; Piauí State, Brazil) are kept in distinct islands (each with approximately 120 m<sup>2</sup>), surrounded by water, but which allows the visualization of individuals from other islands. These primates were exposed to the public and are fed once a day with fruits, vegetables and leaves. Each island has a wooden house (1,5 × 1,5 meters) and perches composed of wooden trunks. There is no record of environmental enrichment activities on these islands. At Parque Estadual Dois Irmãos (PEDI; Recife, Pernambuco State,



**Figure 1.** Sampling areas for the ten groups of *Sapajus libidinosus* included in the study: five groups of free-living animals (Baixa Grande (BG), Jurubeba (JB), Pedra Furada (PF), Oitenta (OT) and Gato (GT)), and five groups living in captivity (Fundação Jardim Zoológico de Brasília (FJZB), Island 1, 2 and 3 of Parque Zoobotânico de Teresina (PZT1, PZT2 and PZT3, respectively) and Parque Estadual Dois Irmãos (PEDI)).

Brazil) the primates are kept in a rectangular screened enclosure, present in the primate wing, approximately 30 m<sup>2</sup> (6 m long, 4.5 m wide and 5 m high) (Appendix 1, Fig. 1), surrounded on one side by trees and on the other by enclosures for other primate species. This enclosure had a brick house (shelter made of masonry of 2 m<sup>2</sup>) to protect the animals against the weather, a shelter made of braided ropes, which allowed greater contact with the external environment, hanging ropes to allow movement throughout the enclosure and dry trunks. The recint is provisioned with fruits, vegetables, ration and leaves twice a day. The food is made available in four hanging feeders located on the sides of the enclosure. PEDI visitors can observe the park fauna four days a week, the other three days of the week, the keepers are destined to carry out environmental enrichment activities with the primates in the enclosure. The Fundação Jardim Zoológico de Brasília (FJZB; Distrito Federal, Brazil) hold the capuchin monkeys on an island of approximately 250 m<sup>2</sup> (Appendix 1, Fig. 1) located in an artificial lake, and exposed to the public six days per week. The primates are fed twice a day with fruits, vegetables and leaves placed in a suspended metal feeder. The centre of the island is equipped with a two-level wooden platform connected to a small shack by perches composed of wooden trunks and rubber bands. A stone den is also present on the island. There is no record of environmental enrichment activities on this island. None of the zoos had detailed information about their origin, time in the zoo, and age at which they arrived at the zoo, of each individual. The only information we have is that all adult individuals were brought from CETAS, coming from trafficking or capture in the urban environment (probably raised as a domestic animal). Juveniles and sub-adults were born at the Zoo. All adult animals were more than three years old at the Zoo.

### Study animals

To test the hypothesis that social behaviour changes in captivity it was not necessary to obtain a complete description of the social organisation at each group. Of course, this complete description could help to interpret the differences between groups in one same condition, but this was not the objective of the present study. Considering that our focus is on social behaviour differences across conditions, we need to have estimates of the social organisation in each group (each unit of analysis) and, accordingly, we sampled 10 groups across the two conditions (free-living vs captivity). To render social behaviour samples comparable across groups, interactions were recorded always in one same, provisioned foraging context. Also, to enhance comparability, all groups were regularly provisioned, and the researcher was always unfamiliar to the animals at the beginning of the experiment. To have an estimative of the social organisation, we selected six individuals at each group, the first seen in each site, with the exception of one group (FJZB, see below) with only five individuals, because one

animal was quarantined during the sampling period. We thus observed a total of 59 individuals, adults and sub-adults of *S. libidinosus* (Appendix 1).

Infants and juveniles were excluded from the sampling in order to avoid age biases. However, when the behaviours were directed from adult/sub-adult to infant/juvenile, they were considered in the analysis. We estimated the age-group of each individual following criteria available in the literature. An individual is regarded as “infant” from birth to independence, when he stops being breastfed and carried out by the mother or other individuals in the group. An individual is regarded as “juvenile” when he is already independent, and as “sub-adult” when he is totally independent but does not show the characteristic body and behavioural development of adults. Finally, an individual is regarded as “adult” when he shows the characteristic body and behavioural development in the case of males and in females after they have their first preceptive period. Females reach sexual maturity when aged three, while males reach sexual maturity at four years old (Izawa, 1980; Torres de Assumpção, 1983; Fragaszy & Adams-Curtis, 1991; Izar, 1994).

### Data collection

The free-living groups were previously habituated to human presence before the onset of the present study. During the habituation process each individual received a name. To identify each individual, we used natural marks, such as tuft size and shape, hair colour, face shape, and scars.

Sampling was conducted with an ethogram adapted from previous studies (*e.g.*, Falótico, 2011; Camargo, 2012), and we performed 19:30 h of observations per group (Altmann, 1974). For the construction of the ethogram, observations made in all the ten groups were taken into account. The resulting ethogram consisted of two behavioural categories, agonistic and affiliative, further subdivided into 10 behavioural elements (Appendix 2). We considered agonistic behaviours those involving threats, attacks, persecutions, bites, as well as those shown in situations of competitive conflicts (*see* Janson, 1985; Bernstein, 1976). Also, we considered affiliative the behaviours promoting the development and maintenance of social ties between the members of the group, for example, allogrooming and playing (*see* Stoesz *et al.*, 2013).

We video-recorded the selected individuals from December/2015 to August/2016. Each group was followed for a period of 7 days, so as to sample each social organisation for one same amount of time, enhancing comparability of the estimative of the level of social interactions across groups. The three groups of Parque Zoobotânico de Teresina were observed between December/2015 and January/2016; the five groups of Parque Nacional Serra da Capivara, between May/2016 and June/2016, in the dry season; the group from Parque Estadual Dois Irmãos, in July/2016; and the group from Fundação Jardim Zoológico de Brasília in August/2016.

We filmed focal animals, between 08:00 h to 17:00 h, for 03:15 hours each individual (continuously), until fulfilling 19:30 h per group, thus comprising a total sampling effort of 191:45 h across the 10 groups.

### Data analysis

Initially one of us (DSSL) decoded the video with the aid of the Software of Analysis of Animal Behaviour – PACCA (Santana *et al.* in development, available under request) and the ethogram of social behaviours (Appendix 2). Considering that most elements in the ethogram are events with negligible duration, the frequency of these elements summarise most of the available information, and accordingly we registered the frequency of the social behaviours (affiliative and agonistic).

The absolute frequency of behaviours corresponding to each activity (grooming, playing, threatening) was transformed into relative frequency, through  $Ci = 100ni/N$ , in order to allow comparisons of the group activity budgets. In the formula, 'n' is the number of records of a given activity 'l' during the period of analysis, and 'N' is the total number of focal activities recorded during the same period (Cullen-Jr. & Valladares-Pádua, 1997).

Group size and the sex of the individuals seemed to correlate with the conditions and, therefore, to ascertain whether these variables were responsible for the observed results, we assessed their possible effects by means of an ANOVA using group size and sex as a factor.

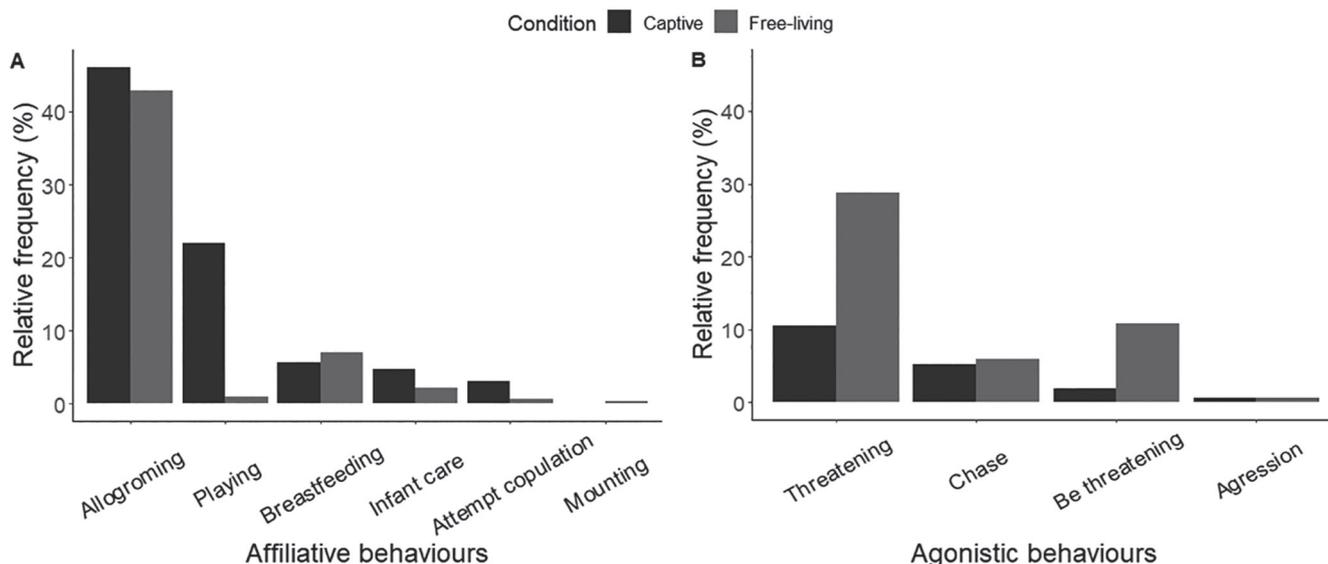
We tested for captive/free-living group differences with a linear mixed model (LMM; Henderson, 1984). The condition (free-living versus captive) was the independent, fixed factor, and the frequency of behaviour (either affiliative or aggressive) the dependent variable. Study sites (PZT1, PZT2, PZT3, PEDI, FJZB, OT, BG, JB, GT, PF) were nested within the fixed effect 'condition', while individuals were nested within their respective groups.

We estimated model parameters and associated statistics through Maximum Likelihood (Fisher, 1922), with a maximum of 1,000 iterations, using the absolute values of log-likelihood (0.00001), parameters (0.000001), and Hessian (0.00001) convergence. The estimative of confidence limits (95%) was performed with 10,000 bootstrap iterations. All analyses were run using IBM® SPSS Statistics v.20 (IBM, 2011) and the software R® v.3.6.0 (R Core Team, 2019), using the nlme (Pinheiro *et al.*, 2019) and lme4 packages (Bates *et al.*, 2015).

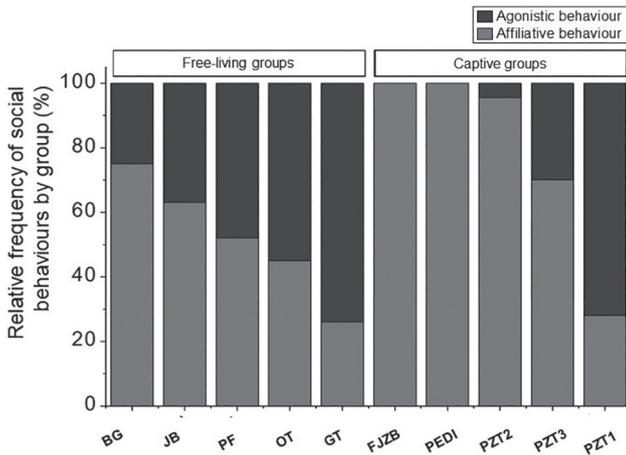
### RESULTS

We recorded a total of 696 behaviours belonging to 10 different social behaviour categories. Together, these behaviours were part of agonistic and affiliative interactions (Fig. 2). In captivity we observed a total of 367 social behaviours, 300 of which were affiliative (Females = 101; Males = 199) and 67 agonistic (Females = 43; Males = 24). In free-living animals we observed a total of 329 social behaviours, of which 173 were affiliative (Females = 100; Males = 73) and 156 were agonistic (Females = 46; Males = 110). Nine types of social behaviours were observed in captivity: five affiliative and four agonistic. Ten types of social behaviours were observed in free-living: six affiliative and four agonistic. Allogrooming was the most frequent affiliative behaviour both in captive (45%,  $N = 165$ , mean = 5.6 by individual,  $SD = 9.04$ ) and in free-living animals (43%,  $N = 139$ , mean = 4.6 by individual,  $SD = 4.67$ ) (Fig. 2). Threatening was the most frequent agonistic behaviour both in captive (10.61%,  $N = 38$ , mean = 1.3 by individual,  $SD = 2.87$ ) and in free-living animals (28.8%,  $N = 93$ , mean = 3.1 by individual;  $SD = 4.07$ ) (Fig. 2).

Free-living groups showed a larger proportion of agonistic behaviours in their social repertoire, when compared to captive groups (Fig. 3). There is large within-condition variation between groups. For example, agonistic



**Figure 2.** Relative frequencies of social activities presented by free-living (Grey) and captive individuals (Black): (A) Affiliative behaviours and (B) Agonistic behaviours. We observed 10 different types of social behaviour, which occurred under both captivity and free-living conditions.



**Figure 3.** Relative frequency of social behaviours for each of the ten studied groups (BG = Baixa Grande; JB = Jurubeba; PF = Pedra Furada; OT = Oitenta; GT = Gato; FJZB = Fundação Jardim Zoológico de Brasília; PEDI = Parque Estadual Dois Irmãos; PZT2 = Parque Zoológico de Teresina (ilha 2); PZT3 = Parque Zoológico de Teresina (ilha 3); PZT1 = Parque Zoológico de Teresina (ilha 1). Under free-living conditions, agonistic behaviours were proportionally more frequent than were affiliative behaviours.

behaviours in the wild corresponded to 55% (N = 52) of all social activities in the OT group, while in the GT group they comprised 74% (N = 34) of the total. There was a strong monopoly of food resources in the GT group, resulting from the behaviour of a single adult male (Itamar) who presented agonistic behaviours whenever a subordinate approached the feeder. In captivity, the animals of PZT1 showed the highest proportion of agonistic behaviours (72%, N = 41) (Fig. 3). This result may be at-

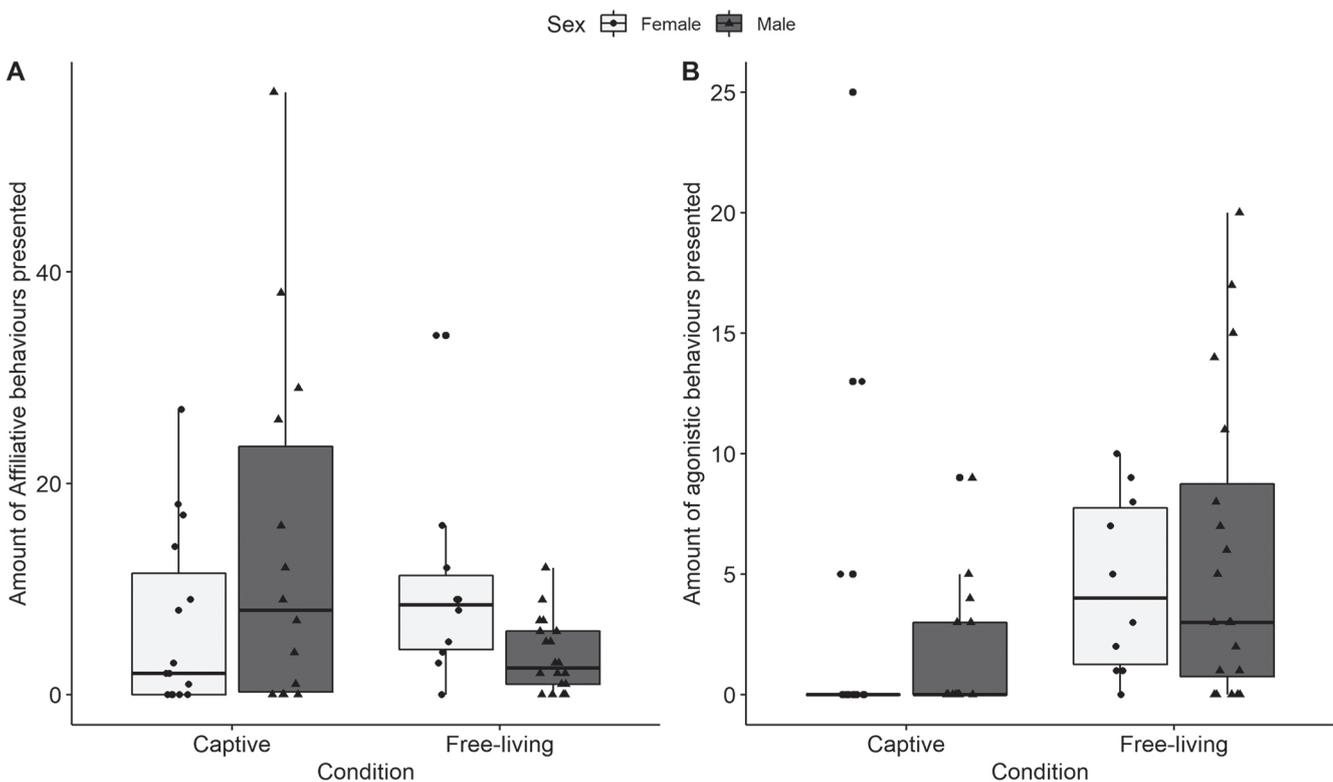
tributed to the behaviour exhibited by a pair of individuals (Juluca and Esaú), which repeatedly threatened each other. Moreover, the alpha male (Hilton) also exhibited threatening behaviours whenever food was provisioned.

There was no difference in affiliative behaviours between free-living and captive animals (N = 59, F = 2.735, p = 0.103, Fig. 4A). Neither group size (N = 59, F = 1.223, p = 0.302) nor sex (N = 59, F < 0.0001, p = 0.989) could explain the overall variability in affiliative behaviour across conditions. Variability within conditions was not explained by group size (free-living: N = 30, F = 0.713, p = 0.589; captivity: N = 29, F = 1.150, p = 0.345), but free-living females exhibited more affiliative behaviour than males (N = 30, F = 7.710, p = 0.009), a finding that did not extend to captive animals (N = 29, F = 2.376, p = 0.134).

Agonistic behaviours were more frequent in free-living than captive groups (N = 59, F = 4.233, p = 0.044, Fig. 4B). Neither group size (N = 59, F = 1.650, p = 0.130), nor sex (N = 59, F = 0.067, p = 0.796) could explain the overall variability in agonistic behaviour. Variability within conditions was not explained by group size (free-living: N = 30, F = 1.338, p = 0.279; captivity: N = 29, F = 0.409) or by sex (free-living: N = 30, F = 0.179, p = 0.676; captivity: N = 29, F = 0.351, p = 0.558).

## DISCUSSION

As suggested by the literature (Janson, 1985; Izar, 1994; Pinha, 2007; Vogel & Janson, 2007), agonistic behaviours were indeed more frequent in free-living than



**Figure 4.** Captivity reduces agonistic interactions and does not change affiliative interactions. (A) Median and quartiles of the frequency of affiliative (A) and agonistic (B) behaviours presented by captive and free-living groups of *S. libidinosus*, separated by sex.

in captive groups of capuchin monkeys (Fig. 4B). The finding that agonistic behaviours decreased in captivity is compatible with a survey from the literature. For example, while in captivity the individuals of *Cebus apella*, *Sapajus nigritus* and *Sapajus apella* spent very small percentages of their activity budget in agonistic activities, usually associated with the onset of food supply (Moro, 2007; Santos & Reis, 2009; Simões, 2013), in natural conditions agonistic behaviours seemed to compose a larger bit of the activity budget throughout the day, also in connection to competition for food (Freese & Oppenheimer, 1981; Isbell & Young, 2002; Izar, 2004; Ferreira *et al.*, 2006; Ferreira *et al.*, 2008; Jaman & Huffman, 2013; Orihuela *et al.*, 2014). The most frequent agonistic behaviour was aggressive threatening. Primates are proficient in resolving conflicts with threats in place of physical fights (van Staaden *et al.*, 2011), as aggressions are costlier and bring the risk of injuries (Strier, 2011).

Contrary to the suggested idea in the literature (Beisner & Isbell, 2008; Lessa, 2009; Jaman & Huffman, 2013; Simões, 2013), we found no effect of captivity on affiliative behaviours in primate groups (Fig. 4A). This discrepancy may have arisen because previous reviews did not conduct systematic comparisons between these environmental conditions, and because no previous study tested empirically the hypothesis that captivity affects social behaviour using the same behavioural metrics across conditions in a paired design, so as to directly collect social data from all groups in one single study. Rather, usually each independent study investigated a single environmental condition (*e.g.*, free-living but not captive groups). For example, while Sussman *et al.* (2005), in their study of 28 genus and 60 primate species, showed that primates living under natural conditions spent less than ten percent of their daily time in affiliative behaviours, others studies showed that captive animals spent most of their daily time in affiliative behaviours (Moro, 2007; Santos & Reis, 2009; Simões, 2013), and the comparison of these independent studies could prompt one to the conclusion that affiliative behaviour increases in captivity. Nevertheless, strictly, this conclusion does not follow from this superficial comparison of results. Different studies use different ethograms, different observers, different sampling methods, different species, at different seasons, years or decades, and a true systematic comparison would have to statistically control at least the major differences across these studies to provide a valid conclusion.

Grooming was the most frequent affiliative behaviour across conditions (Fig. 2), corroborating previous reports (*see* Sussman *et al.*, 2005). Grooming seems to serve many functions. Monkeys use grooming to form coalitions (Rose, 1998; Tiddi *et al.*, 2011), in addition to serving as an affiliate strategy for the purpose of relieving agonistic events (Tiddi *et al.*, 2011), it also serves to establish and strengthen affective bonds (Sparks, 1967; Seyfarth, 1977; Gillam, 2011), in addition to promoting social cohesion (Yamamoto, 1991). Such functional diversity in a single behavioural modality could partially explain why grooming was carried out at comparable levels under

both captive and free-living conditions: some functions could be relevant in captivity, while others could be relevant for free-living groups. Considering that aggressiveness was more frequent in the wild, it could be the case that grooming would mostly play the function of reconciliation in the wild, while being used mostly for cleaning or for coping with chronic stress in captivity. (Lima, 2011; Sonnweber *et al.*, 2015; Wooddell *et al.*, 2017; Yamanashi *et al.*, 2018).

Sex did not explain the overall variability in affiliative behaviour. Sex is considered a factor with a known influence on social behaviour in primates (Irwin & Ehardt, 1985; De Waal & Luttrell, 1986). Despite this, free-living females were more affiliative than free-living males (Fig. 4). In relation to sex, females tend to remain more in proximity (Perry, 1996) and do more picking among themselves (O'Brien, 1991; Perry, 1996, Di Bitetti, 1997). In relationships between males and females, in affiliation behaviours males are more responsible for maintaining dyadic proximity (Perry, 1997), while females generally do more picking, especially in the alpha male (Tiddi *et al.*, 2012).

Although we cannot point to specific differences across free-living and captive conditions that could be causally connected to these results, we could statistically rule out group size and sex as potential factors. Still, a variety of other factors could potentially explain these results. Primates modulate their behaviour in response to changes in food resources (Southwick, 1967; Janson, 1985; Izar, 1994; Phillips, 1995; Casanova, 2006; Pinha, 2007; Vogel & Janson, 2007; Ferreira *et al.*, 2008; Beisner & Isbell, 2008; Lessa, 2009), space availability, structural complexity and stimulus diversity (Morgan & Tromborg, 2007), the presence of visitors (Hosey, 2005), or even to changes in the actual possibility of control over daily routines (*e.g.*, patrolling large distances may be sometimes impossible), or in the actual possibility of choosing social partners (Machairas *et al.*, 2003; Morgan & Tromborg, 2007; Scott & Lockard, 2007). Overall, these factors could make captivity a potentially less stimulating context for primates (Simões, 2013).

From the many factors that could explain the relatively higher proportion of agonistic interactions in the wild (Fig. 3), relative food scarcity during the dry season in tropical dry forests (Caatinga), associated with an insufficient, partial food supply provided for free-living groups, could possibly be the most important. Food supply strongly affects primate social behaviour (Carpenter & MacMillen, 1976; Wolf, 1978; Janson, 1985; Izar, 1994; Phillips, 1995; Pinha, 2007; Vogel & Janson, 2007; Ferreira *et al.*, 2008; Izar *et al.*, 2012), and considering that food monopolisation was facilitated by provisioning in the feeders, the monopolisation of a scarce food resource could potentially be at the root of increase agonistic interactions (Janson, 1985; Boccia *et al.*, 1988; Isbell, 1991; Sterck & Steenbeek, 1997; Pellegrini *et al.*, 2007; Pellegrini, 2008; Huntingford & Chellappa, 2011; Back *et al.*, 2019; Overduin-de-Vries *et al.*, 2020).

On the other hand, it is worth considering that, in captivity, due to the limited space (including the height

of the enclosure in the PEDI), individuals tend to “avoid conflict”, and thus captive individuals tend to become more tolerant. Primates living in captive conditions increase the rate at which they perform conflict-reducing responses in order to minimize the amount of aggression, increasing, for example, grooming to calm others and increasing friendly affiliate behavior to reduce social tension (De Waal, 1989; Judge & De Waal, 1997; Mitani & Waats, 2001; Judge *et al.*, 2006). Fragasz *et al.* (2004) found differences between captive males, indicating high standards of tolerance and suggesting that, when in a group, they can live in captivity for years and not even have a single physical agonistic event.

Considering that *S. libidinosus* has an ample geographic distribution (Rylands *et al.*, 2013), the present results could be extended in generality with the addition of wild groups from other geographic areas, particularly populations from other biomes, such as Atlantic forest and Cerrado (Savannah). Also, a more thorough sampling of groups, and of social behaviour within each group, would help to tease apart the multiple factors that could explain the resulting pattern, while also allowing to pinpoint factors that are actually driving the variability within each condition.

## CONCLUSION

Captivity had indeed an impact on social behaviours. As expected, it entailed a reduction in agonistic interactions in *S. libidinosus*. Nevertheless, and contrarily to prevailing interpretations based on previous studies, captivity did not affect affiliative interactions. We thus found no evidence for the hypothesis that captivity leads to an increase in affiliative behaviours. Future studies should focus on the specific mechanisms underlying the findings reported here. Although group size and sex did not explain social behaviour variability across conditions, we found mixed evidence concerning the interaction between sex and condition, and so experiments designed specifically to disentangle and test these and other putative factors would clarify the details of these interactions.

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## APPENDIX 1

Number of individuals, name, sex, age and origin of capuchin monkeys observed for this study in captive and wild conditions. (\* Alpha male).

Environment	Place	Geographical coordinate	Number of individuals	Individual	Sex	Age range
Free-living	Baixa grande (BG)	08°88'790"S; 42°65'198"W	44 individuals	Dan*	Male	Adult
				Leticia	Female	Adult
				Hortência	Female	Adult
				Manchado	Male	Subadult
				Toim	Male	Adult
	Gato (GT)	08°86'260"S; 42°61'324"W	24 individuals	Valtim	Male	Subadult
				Poca Zói*	Male	Adult
				Chifre	Male	Subadult
				Itamar	Male	Adult
				Preta	Female	Adult
	Jurubeba (JB)	08°86'790"S; 42°60'855"W	35 individuals	Thor	Male	Adult
				Topetuda	Female	Adult
				Barba*	Male	Adult
				Arrepiada	Male	Adult
				Beto	Male	Adult
	Oitenta (OT)	08°87'416"S; 42°63'263"W	66 individuals	Fernandinha	Female	Adult
				Máscara	Male	Subadult
				Soneca	Male	Subadult
				Bolinha*	Male	Adult
Bianca				Female	Adult	
Pedra Furada (PF)	08°83'223"S; 42°55'180"W	36 individuals	Clarinha	Female	Adult	
			Panaca	Male	Adult	
			Pelé	Male	Subadult	
			Loirão	Male	Adult	
			Zandor*	Male	Adult	
Parque Zoológico de Teresina (PZT1)	05°02'301"S; 42°46'097"W	8 individuals	Mala	Male	Subadult	
			Roger	Male	Adult	
			Torto	Male	Adult	
			Vesga	Female	Adult	
			Encrenqueira	Female	Adult	
Parque Zoológico de Teresina (PZT2)	05°02'301"S; 42°46'097"W	7 individuals	Hilton*	Male	Adult	
			Carol	Female	Adult	
			Daniel	Male	Adult	
			Esau	Male	Subadult	
			Juluca	Female	Adult	
Parque Zoológico de Teresina (PZT3)	05°02'301"S; 42°46'097"W	6 individuals	Juma	Female	Adult	
			Gabi	Female	Adult	
			Zangado*	Male	Adult	
			Layolle	Female	Adult	
			Léo	Male	Subadult	
Fundação Jardim Zoológico de Brasília (FJZB)	15°51'026"S; 47°56'160"W	5 individuals	Michelly	Female	Subadult	
			Galego	Male	Adult	
			Gustavo*	Male	Adult	
			Cleslei	Male	Subadult	
			Fran	Female	Adult	
Parque Estadual Dois Irmãos (PEDI)	08°00'376"S; 34°56'414"W	8 individuals	Sidieres	Male	Subadult	
			Rayane	Female	Adult	
			Zé	Male	Subadult	
			Rodrigo*	Male	Adult	
			Thaise	Female	Adult	
Fundação Jardim Zoológico de Brasília (FJZB)	15°51'026"S; 47°56'160"W	5 individuals	Dengoso	Male	Subadult	
			Eliete	Female	Adult	
			Mona	Female	Adult	
			Sapeca	Male	Subadult	
			Chico*	Male	Adult	
Fundação Jardim Zoológico de Brasília (FJZB)	15°51'026"S; 47°56'160"W	5 individuals	Luciana	Female	Adult	
			Olivia	Female	Adult	
			Pretinha	Female	Adult	
Fundação Jardim Zoológico de Brasília (FJZB)	15°51'026"S; 47°56'160"W	5 individuals	Clara	Female	Adult	

## APPENDIX 2

Ethogram for behavioural data collection of *Sapajus libidinosus*, adapted from Santos & Reis (2009), Gouveia (2009), Verderane (2010), Martins (2010), Cutrim (2013), Rodrigues (2014), and Oliveira (2014).

Category	Behaviours: description
<b>Agonistic behaviours</b>	<p><b>Threatening:</b> The individual may move forward while forcefully tapping things around him/her. Generally, this behaviour comes with vocalisations, while standing in a quadruped posture, with the tail standing upward and staring at the threatened conspecific.</p> <p><b>Be threatened:</b> Threatened individual runs away from an aggressor and vocalises, then sits and hugs his/her own tail while raising his/her eyebrows in the direction of the possible aggressor.</p> <p><b>Aggression:</b> An individual pushes, beats and/or bites a conspecific.</p> <p><b>Chase:</b> The individual run after a conspecific. Maybe accompanied with vocalisations of type mobbing calls.</p>
<b>Affiliative behaviours</b>	<p><b>Allogrooming:</b> When an individual manipulates the hair of the other using hands, tongue or teeth, doing this often.</p> <p><b>Playing:</b> Two or more individuals stay rolling on the ground and/or running, chasing each other and/or pretending to bite.</p> <p><b>Infant care:</b> An individual (male or female), carries an infant on its own back.</p> <p><b>Mounting:</b> Performed by two same-sex conspecifics, whereby an individual rides on top of the other making repetitive copulation-like movements.</p> <p><b>Breastfeeding:</b> A female individual feeds an infant with milk. Usually the pup is clinging to the belly and with the mouth on the female's nipples.</p> <p><b>Attempt copulation:</b> A male mount on female, but there is no penetration of the vagina.</p>